Histological data on bone and teeth in two dragonfishes (Stomiidae; Stomiiformes): *Borostomias panamensis* Regan & Trewavas, 1929 and *Stomias boa* Reinhardt, 1842

by

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Abstract. – The predatory mesopelagic fishes *Borostomias panamensis* and *Stomias boa* (Stomiidae) have typical sharp long fangs. The cross section of their teeth shows that the dentinous wall of the pulp cavity is smooth, contrary to the pleated wall found in several predatory fishes like e.g., *Hoplias aimara* (Erythrinidae), *Anarhichas denticulatus* (Anarhichadidae) or *Lophius piscatorius* (Lophiidae). Therewith, *B. panamensis* and *S. boa* lack the plicidentine layer in their teeth. We further confirm the acellular nature of the bone in Stomiidae, already signalled in 1859 by Kölliker for *Chauliodus*.

Résumé. – Données histologiques sur l'os et les dents de deux poissons-dragons (Stomiidae, Stomiiformes) : *Borostomias panamensis* Regan & Trewavas, 1929 et *Stomias boa* Reinhardt, 1842.

Les deux espèces prédatrices, mésopélagiques, *Borostomias panamensis* et *Stomias boa* (Stomiidae), ont des dents effilées et pointues caractéristiques. Les parois de dentine de la cavité pulpaire ne sont pas plissées contrairement aux dents caniniformes de plusieurs autres téléostéens prédateurs tels que *Hoplias aimara* (Erythrinidae), *Anarhichas denticulatus* (Anarhichadidae) ou encore *Lophius piscatorius* (Lophiidae). Donc *B. panamensis* et *S. boa* n'ont pas de plicidentine dans leurs dents. Par ailleurs, nous confirmons l'acellularité des tissus osseux des Stomiidae, une caractéristique histologique signalée une première fois par Kölliker, en 1859, pour *Chauliodus*.

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The barbeled dragonfishes (Stomiidae) are characterized by a luminescent chin barbell. They are found worldwide in the meso- and bathypelagic depth (Tchernavin, 1953; Gibbs, 1969; Clarke, 1974; Nelson *et al*., 2016). They mainly feed on fishes, but some species also feed on crustaceans and cephalopods (Sutton and Hopkins, 1996; Williams *et al*., 2001). They display astonishing anatomical specializations such as an enlarged occipito-vertebral gap where only the notochord persists and extensible stomachs to swallow large prey items (Tchernavin, 1953; Fink, 1985; Schnell *et al*., 2008, 2010; Schnell and Johnson, 2017). They further possess elongated upper and lower jaws with long and sharp fangs (Tchernavin, 1953; Greven *et al*., 2009).

The presence of dentine pleats in the pulp cavity, the so-called plicidentine, has long been considered a character of Sarcopterygii (Schultze, 1969, 1970; Kerney and Rieppel, 2006; Maxwell *et al*., 2011; and others). It has further been described to be present in the teeth of the basal actinopterygian family Lepisosteidae (Tomes, 1878; Peyer, 1968; Schultze, 1969; Meunier and Brito, 2017). Meanwhile, recent studies have shown that a relatively simple pleating of the dentine wall, the so-called "simplexodont plicidentine" (Meunier *et al*., 2015a), is developed in the pulp cavity of teeth of polypterids and amiids (Germain and Meunier, 2017), two other basal Actinopterygian taxa, and also in a series of predatory teleostean fishes from various freshwater and marine environments: *Arapaima gigas* (Schinz, 1822) (Arapaimatidae), *Chitala chitala* (Hamilton, 1822) (Notopteridae), *Hyperopisus bebe* (Lacepède, 1803) (Mormyridae), *Hoplias aimara* (Valenciennes, 1847) (Erythrinidae), *Dissostichus eleginoides* Smitt, 1898 (Nototheniidae), and *Lophius piscatorius* Linnaeus, 1758 (Lophiidae) (Meunier *et al*., 2013; Meunier, 2015; Germain *et al*., 2016). So far, the presence of this dentine type is assumed as a mechanical answer to prey grabbing behaviour that thus appears convergent in different lineages (Meunier, 2015; Meunier *et*

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al., 2015a, b; Germain *et al*., 2016). However, we still lack sufficient data to support this hypothesis. The purpose of the present study is to further explore tooth histology in predatory teleosts with the case of mesopelagic marine stomiid fish that exhibit high and sharp teeth, check whether they display or not pleats in the pulp cavity of their teeth and relate this with their feeding behaviour.

So far, the most comprehensive study on stomiid teeth, investigating *Chauliodus sloani* Bloch & Schneider, 1801, was published by Greven *et al*. (2009); but they do not mention the presence or absence of pleated walls in the pulp cavity of this species (but they illustrated teeth lacking plicidentine). Moreover, while Kölliker (1859) described the presence of acellular bone in stomiids, *i.e*. in *Chauliodus sloani*[1] and *Stomias boa boa*[2], no illustration is available to document, here or elsewhere, stomiid jawbone histology. So, in the present study, we complement the investigation of the tooth organization and histology in two stomiid species, *Borostomias panamensis* Regan & Trewavas, 1929, and *Stomias boa* Reinhardt, 1842, with the histology of their jaw bone.

MATERIAL AND METHODS

Material

Examined specimens are deposited in the following institutions: Scripps Institution of Oceanography, USA (SIO); Museum of Comparative Zoology, Harvard University, USA (MCZ); Muséum national d'Histoire naturelle (MNHN).

Borostomias panamensis: one specimen (SIO 65-188), 125 mm TL (histological sections).

Stomias boa: one specimen (MCZ 129070), 62 mm TL (histological sections); one specimen (MNHN-2015.0147), 145 mm TL (CT-scan imaging); one specimen (MCZ 129070), 43 mm TL (cleared and double stained).

Methods

Cleared and stain preparation

One specimen of *Stomias boa* was cleared and double-stained with Alcian blue and Alizarine red (Dingerkus and Uhler, 1977). The head of the specimen was photographed with a Canon 300D digital SLR camera attached via a LM digital adapter to a stereomicroscope (Zeiss Stemi 2000 C) and compound microscope (Olympus).

Thin section preparation

The heads of *Borostomias panamensis* and *S. boa* were embedded in Paraffin, cut in 15-µm thick serial sections, and stained with Azan (Domagk, 1933). The sections were examined with a microscope Olympus BX51 and photographed with a Leica MC 170 camera.

Non destructive X-ray tomography

The teeth and their supporting bone were X-rayed utilizing a Computed Tomography (CT) imaging system (AST-RX platform and Ge Sensing and inspection Technologies phoenix-ray v|tome|x L240-180 CT scanner) at the Muséum national d'Histoire naturelle, with microfocus RX 180kV/15W source and a 400 × 400 mm detector with a matrix of 2024 pixels (pixel size: 200 × 200 µm). 2000 images were acquired with the following scan parameters: voltage 72KV, current 220 µA, exposure 500 ms, voxel size 10.36 µm. The micro-CT data were processed utilizing *datos|x* reconstruction software (Phoenix|x-ray, release 2.0) and then exported as a 16 bits TIFF image stack. VG studio max software (Volume Graphics, release 2.2) was used for the virtual slice visualization and 3D rendering.

RESULTS

Tooth anatomy and morphology

The two studied species have long and sharp teeth (Fig. 1) inserting on the elongated jawbones, that are weakly curved inwards (Figs 1, 2A). There is only one row of teeth on each jaw and the teeth are separated from each other by relatively large empty spaces (Fig. 1). Here and there, smaller teeth are ankylosed to the jaws (Fig. 2), while the partially

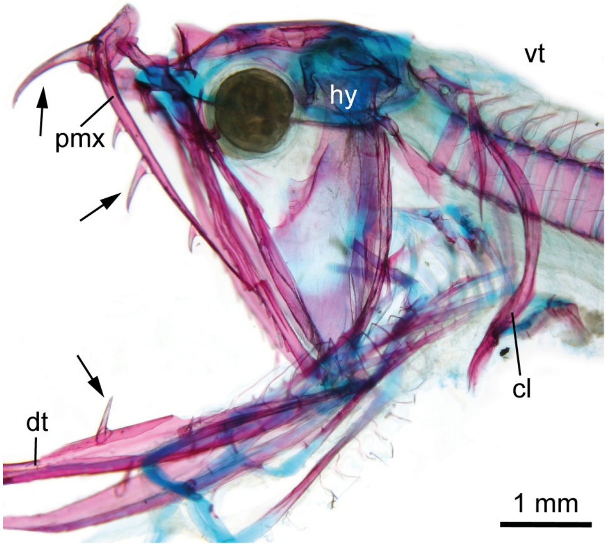

Figure 1. – *Stomias boa*. Cleared and double-stained specimen. Lateral view of the skull showing the jaws with their long sharp teeth (arrow-heads), the suspensorium, the shoulder girdle, and the anterior part of the vertebral column. cl: cleithrum; dt: dentar; hy: hyomandibular; pmx: premaxillary; vt: vertebral column. Scale bar = 2 mm.

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[1] Named *Chauliodus* "*setinotys*" in Kölliker (1859).

[2] Named *Stomias barbatus* in Kölliker (1859).

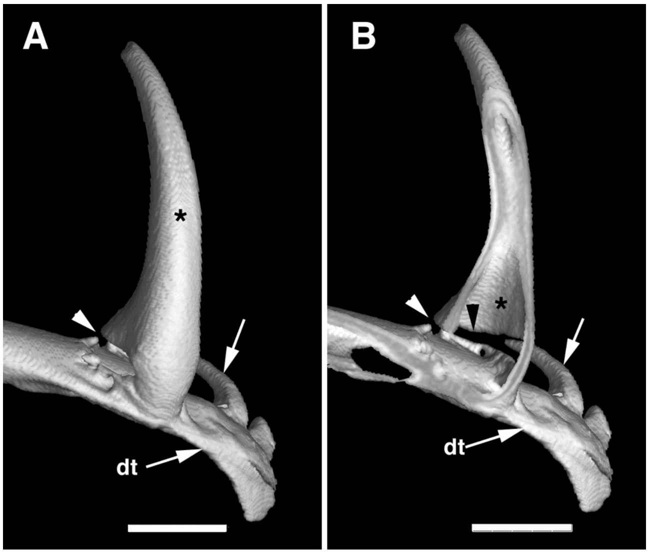

Figure 2. – *Stomias boa*. Tomographic imaging of the right jaw. **A**: Three-dimensional reconstruction of the external (labial side) anterior part of the jaw, showing a caniniform tooth. The external surface of the tooth is smooth (asterisk). The arrowhead and the arrow point to the unmineralized ligament of the fang and to a small tooth, respectively. **B**: Virtual parasagittal section of the anterior part of the jaw showing the pulp cavity of the same tooth than in Fig. 2A. The walls of the pulp cavity are perfectly smooth (asterisk). Both arrowheads point to the unmineralized ligament of the tooth. Dt: dentar. Scale bars = 1 mm.

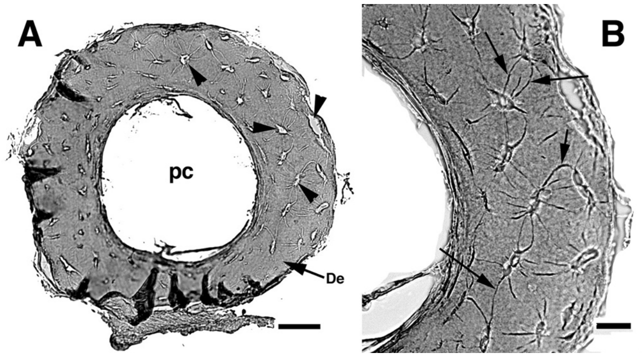

Figure 3. – *Borostomias panamensis* (Azan). **A**: Cross section of a caniniform tooth showing the dentine core (De) and the pulp cavity perfectly circular (pc). In the dentinous tissue, numerous sections of vascular canals are seen (arrowheads). **B**: Detail of figure 3A. The vascular canals are surrounded by numerous canalicles more or less ramified (arrows), and that housed odontoblastic processes. Scale bars: A = 50 µm; B = 20 µm.

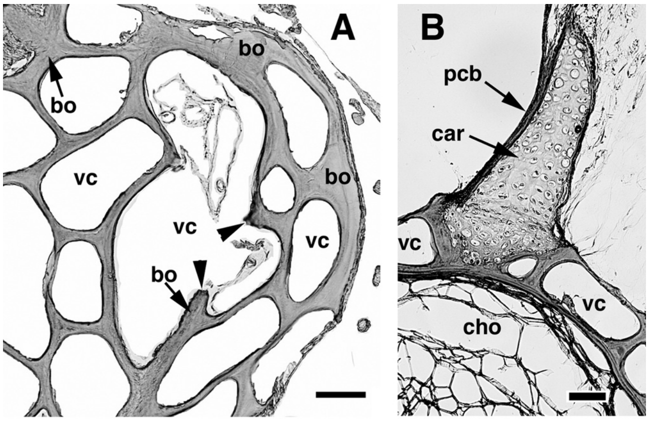

Figure 4. – *Borostomias panamensis* (Azan). **A**: Section of a visceral arch showing the numerous vascular cavities (vc) limited by relatively thin bony trabeculae. No embedded osteocytes are seen in the bony tissue (bo). The two arrowheads point to resorbing bone. **B**: Cross section of a vertebra showing a cartilaginous neural arch fused to the bony vertebral centrum. The cartilaginous tissue (car) is surrounded by a perichondral layer (pcb) of acellular bone. cho: chordal tissue: vc: vascular cavity. Scale bars: A = 50 µm; B = 50 µm.

hinged teeth are incompletely fused to their bony support (Fig. 2; type 3 of tooth attachment in Fink (1981) typology). The ligament that fixes the tooth to the jaws on its lingual side is not mineralized (Fig. 2B) contrary to the labial side. This peculiarity should permit depression of teeth during prey capture, after which they retake their posture to prevent escaping of prey that can then be swallowed. From their base to their apex the teeth have a smooth external and internal surfaces (Fig. 2A, B).

Tooth histology

X-ray tomography and the following 3D models show that the wall of the pulp cavity is perfectly smooth without pleats (Figs 2B, 3A). The histology further shows that the dentine is crossed by axial vascular canals (Fig. 3A), from which odontoblastic canalicles ramify into the dentinous tissue (Fig. 3B). These canalicles house cytoplasmic processes of the odontoblasts. This histological organization is characteristic of osteodentine (Ørvig, 1967; Peyer, 1968; Schmidt, 1971; Huysseune and Sire, 1998).

Bone histology

The bony tissues of the jaws and of the vertebral column in *Borostomias panamensis* and *Stomias boa* lack embedded osteocytes (Fig. 4). They therewith possess acellular bone (= anosteocytic bone of Weiss and Watabe, 1979). We did not observe osteoblastic canalicles (Fig. 4) in the acellular bone of both investigated stomiids. The observed bones (skull and vertebrae) are constituted of relatively thin bony trabeculae that wrap large vascular cavities (Fig. 4A, B). Here and there, minute resorption of bony tissue is observed (Fig. 4A).

DISCUSSION – CONCLUSION

Dentinous tissue of *Borostomias panamensis* and *Stomias boa* is typically an osteodentine. A similar condition has been described for *Esox lucius* Linnaeus, 1758 (Herold and Landino, 1970; Herold, 1971; Texereau *et al*., 2018), and

Lepidopus caudatus (Euphrasen, 1788), *Sphyraena guachancho* Cuvier, 1829 and *Thyrsites atun* (Euphrasen, 1791) (Texereau *et al.*, 2018) among others.

Our study shows that the sharp long fangs of *Borostomias panamensis* and *Stomias boa* lack a plicidentine organization contrary to what is observed in several predator teleosts (Meunier *et al.*, 2013; Bemis and Bemis, 2015; Meunier, 2015; Germain *et al.*, 2016; Meunier and Germain, 2018). We therewith confirm the illustration of stomiid teeth of Greven *et al.* (2009, Fig. 2E) where the walls of the pulpar cavity in teeth of *Chauliodus sloani* lack pleats. Most Stomiidae are considered to be efficient predators, feeding on large prey items relative to their own body length (Tchernavin, 1953). The lack of plicidentine in their teeth contradicts a direct relationship between the diet and this tooth feature. Because the teeth of *S. boa* and *B. panamensis* are slender and their pulp cavity is relatively narrow, we suggest that this anatomical peculiarity may prevent the pleating of the dentinous wall of the pulp cavity. Moreover, the depression of the teeth during prey catching (Fink's type 3 tooth attachment; Fink, 1981), facilitated by an incompletely mineralized area at the base of teeth, would be difficult if the teeth possessed a plicidentine organization. Finally, since Stomiidae engulf their prey by suction feeding (Tchernavin, 1953), their alternating teeth of the upper and lower jaws resemble a cage and probably prevent escaping of the prey. Therewith their fangs are not submitted to the same mechanical constraints and pleating of the walls of the pulp cavity is possibly not useful like in certain other predatory fish such as *Hoplias*. The lack of simplexodont plicidentine in stomiid thus does not contradict the fact that this corresponds to a mechanical adaptation to biting constraints (Meunier, 2015; Meunier *et al.*, 2015a, b; Germain *et al.*, 2016) and puts in light the variety of predation behaviours and adaptations.

Moreover, complementary information on jawbone histology shows the acellular nature of bony tissue in the Stomiidae, and confirms Kölliker (1859) description for *Chauliodus sloani* and phylogenetic distribution of this feature in the large majority of ectothermic fishes (Davesne *et al.*, 2018, in press). Here, we also have noticed the absence of osteoblastic canalicles in the acellular bone of *Borostomias panamensis* and *Stomias boa*. In case osteoblastic canalicles are present they possibly participate in the nutrition of bony tissue (Sire and Meunier, 2017). In stomiids, nutritive elements might enter the thin bone from the surrounding vascular spaces. Similar observations were made in other deep-sea fishes like the rift eelpout *Thermarces cerberus* (Meunier and Arnulf, 2018), and in various Antarctic notothenioid fishes from the whole water column (Eastman *et al.*, 2014).

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